Rhizosphere in space and time – challenges for designing the most relevant root traits for efficient nutrient acquisition

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INTRODUCTION

The rhizosphere, i.e. the soil volume that is influenced by the activities of living roots, has been largely documented for its pivotal role in plant nutrition, and thus ecological significance in terrestrial ecosystems (e.g. Hinsinger et al., 2009). The number of studies on the fate of nutrients in the rhizosphere, especially phosphorus amongst major nutrients, iron and zinc amongst micronutrients, has considerably increased over the past decades, as revealed by the published literature. However, much of our understanding of the underlying rhizosphere processes rely on microcosm experiments in more or less artificial conditions. In contrast, we still lack comprehensive studies of the rhizosphere of field-grown plants that includes both its spatial and temporal dimensions. The aim of this keynote lecture is to address these two facets that challenge our capacity to predict plant nutrition and to manipulate such rhizosphere properties for the purpose of an ecological intensification of agroecosystems.

SPATIAL DIMENSIONS OF THE RHIZOSPHERE

A major trait of the rhizosphere is that its radial extension considerably vary according to the root activity that is considered (Hinsinger et al., 2005; Gregory, 2006), which is largely related to the varying mobility of various types of root exudates and soil resources (water and nutrients) as well established by modelling approaches (Barber, 2005; Raynaud et al. 2008). For instance, poorly mobile nutrients such as phosphate or micronutrients are expected to diffuse over short distances, in the millimetric range, while more mobile nutrients such as nitrate can be accessed by roots at several centimeters of the root surface. Based on such differences, recent root architecture modelling (Pagès, 2011) has shown that continuously increasing the value of a root trait such as root length is always beneficial for a poorly mobile nutrient such as phosphate or, to a lesser extent potassium, while it is useless for more mobile resources (water or nitrate). However, this model does not account for mycorrhizal hyphae and their contribution to increase the access to remote phosphate ions in the bulk of the soil. The model developed by Schnepf et al. (2008) confirmed the microcosm experiments designed by Jakobsen et al. (1992) that showed that arbuscular mycorrhizal hyphae can expand the volume of the phosphate depletion zone to a distance of several centimeters from the root surface. It is still an open question in real world conditions, accounting for the 3D development of depletion zones around active parts of the root system and its spatial extensions such as mycorrhizal hyphae or root hairs. A recent paper has been published by Roose et al. (2013), providing an estimate of the relative contribution of root hairs to phosphorus acquisition when accounting for a realistic distribution of root-soil and root hair-soil contacts in a natural, complex (aggregated) soil sample. In their case study which stands for a single piece of soil and plant genotype, root hairs' contribution to phosphorus acquisition was estimated to 50%. This kind of approach would be valuable to pursue for better quantifying the actual role of mycorrhizal hyphae. Such feature explains why phosphorus depletion has been often shown to occur over greater distance than expected. Other root traits such as those determining the release of nutrient-mobilizing compounds of varying mobility are to be considered as well. These ultimately result in the creation of a highly heterogeneous soil environment at the microscale of the rhizosphere of the whole root system, as evidenced with novel techniques used to probe soil properties such as the optical sensors (optodes) used by Blossfeld et al. (2013) to map rhizosphere pH. When talking about the spatial dimension of the rhizosphere, it shall be emphasized that most of what we currently know has been established for roots growing in the topsoil, while there are only few studies on deeper roots, in spite of their relevance in water and nutrient acquisition, especially in low input agroecosystems. This is another challenge for further understanding of plant nutrition.

TEMPORAL DEVELOPMENT OF THE RHIZOSPHERE

Compared to its spatial dimension, the temporal dimension of the rhizosphere is even less studied, largely because of the lack on non-invasive approaches. Some studies have attempted to measure rhizosphere properties at various periods (seasons or growth stages), but most of the published literature correspond merely to snapshots of the root environment in the life of a plant, and we actually know very little about the fate of rhizosphere processes. Here again the recent development of non-invasive sensors such as optodes can help us understanding short term changes of rhizosphere properties such as soil pH or pO_2 (Blossfeld et al., 2013; Schreiber et al. 2012) that are known to play a key role in determining the availability of e.g. phosphate and micronutrients. A technical challenge is to implement such technologies in field grown plants with minimal disturbance. There is no doubt that modelling will thus be a major tool to address this issue of the temporal development of the rhizosphere for realistic root systems of growing plants. Walter et al. (2009) stress that most models are root-centered while it would be valuable to address this issue of rhizosphere development at the viewpoint of the soil: while root apex is moving fast, soil particles remain at the same location and experience over time the contact with root tip and then progressively older sections of the growing root. The rhizosphere, as the root, becomes progressively older, at any given point along the root system. There are very few studies that have been designed to tackle this issue properly, as e.g. that of D'Angelis et al. (2009) when studying the composition of microbial communities in the rhizosphere. Former studies had been indicating changes of microbial communities over time by sampling the whole root system and adhering soil at various stages of plant development (e.g. Mougel et al., 2006). The challenge is now to relate such temporal changes to the fate of nutrients and its ultimate impact on the whole plant nutrition.

CONCLUSIONS

In spite of the considerable number of studies on the rhizosphere, very few adequately address its spatial, and even less so temporal development. This questions the ability of our models to properly predict plant nutrition and design efficient ideotypes or genotypes for improved nutrient acquisition efficiency. Lynch (2007) nicely pointed the need to better account for root growth/architecture and rhizosphere-related traits to search for plant genotypes that better cope with low input agriculture. But we are still far from identifying what would be the best combination of traits to face multiple stresses such as drought combined with limiting availability of either nitrogen or phosphorus, to name just these two major nutrients. While roots grow through the soil, rhizosphere develops in space and time and ultimately create a complex set of microniches for microbial communities including those that can play a significant role in altering root growth and nutrient acquisition. As stressed recently by Bakker et al. (2012), when aiming at designing strategies to improve crop yield while reducing chemical inputs such as fertilizers, direct manipulations of soil microbial communities (via e.g. the inoculation of beneficial microorganisms) is less likely to prove efficient than plant-based strategies to design or breed plant genotypes that will locally promote the targeted rhizosphere microbiome (e.g. nutrient solubilizers, or plant growth promoting organisms). This strategy is certainly a clue to a successful ecological intensification of agroecosystems.

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